THE FEEDING MECHANISMS AND AFFINITIES OF THE TRIASSIC BRACHIOPODS *THECOSPIRA* ZUGMAYER AND *BACTRYNIUM* EMMRICH

by M. J. S. RUDWICK

ABSTRACT. The morphology of *Thecospira* and *Bactrynium* is analysed functionally. It is inferred that the spiral brachidium of *Thecospira*, with its unique grooved lamellae, bore a simple spirolophe, and that the 'lobate apparatus' of ridges and grooves in *Bactrynium* bore a complex ptycholophe. The morphology of both genera is consistent with ciliary feeding mechanisms similar to those of living brachiopods: it is inferred that *Thecospira* operated a spirolophous current system of 'exhalant' or 'spirifer' type, analogous to the living *Discinisca*; and that *Bactrynium* operated a ptycholophous system analogous to the living *Megathiris*. Both brachiopods were cemented in early growth stages but later became free-lying; both had a strophic hinge, and normal articulation and musculature. *Bactrynium* is pseudopunctate, *Thecospira* includes punctate and impunctate (or obscurely pseudopunctate) species. Affinity with Permian Davidsoniacea is accepted for *Thecospira*; the nature of its derivation is discussed in functional terms. *Bactrynium* is assigned to the Thecideacea; its resemblance to Permian Lyttoniacea is interpreted as due to functional convergence. It is concluded that the Thecideacea were derived from Davidsoniacea, probably during Permian time and probably by neoteny; affinity to Spiriferida or Tere-bratulida is thus rejected, and the older view reaffirmed, that Thecideacea are surviving Strophomenida. The phylogenetic history of the feeding mechanisms of Thecideacea and *Thecospira* is interpreted in terms of a concept of 'functional zones', and is regarded as an example of 'size-required allometry'.

THE small and rare Triassic brachiopods *Thecospira* and *Bactrynium* are of special interest in the study of the functional evolution of the phylum. Of all the changes in brachiopod faunas between the late Palaeozoic and the early Mesozoic, the most striking is the almost complete disappearance of the Strophomenida. Strophomenides were abundant and diverse in the Permian period, but their representatives in the Triassic are rare, and so changed in form that their affinities have remained controversial.

One such relict strophomenide is the Middle to Upper Triassic *Thecospira*. Its strophomenide affinities are now generally recognized, and it is regarded as the only known post-Palaeozoic davidsoniacean (Williams 1953a, 1965). But it has undergone significant morphological changes, of which the most important is its acquisition of a spiral brachidium with grooved lamellae.

Another relict strophomenide, the late Triassic (Rhaetian) *Bactrynium*, is more problematical. It has a concavo-convex shell resembling that of many Palaeozoic strophomenides. The interior of the dorsal valve bears a series of multi-lobed ridges and grooves which give it a striking resemblance to the Permian lyttoniacean *Oldhamina*. On the other hand it was originally regarded as being related to the post-Palaeozoic thecideaceans. The functional analysis of *Bactrynium* in this paper is designed to help to distinguish more clearly those characters that are likely to be due to affinity from those that result from functional parallelism or convergence.

Discussion of *Thecospira* and *Bactrynium* naturally bears on the controversial problem of the affinities of the thecideaceans. Williams's and Rowell's recent contribution to this

problem (1965, pp. H187–9) seems to over-stress features indicating possible affinity to spiriferides or terebratulides, at the expense of those that have previously suggested a connexion with the strophomenides. I believe that a strophomenide affinity for the thecideaceans should be given further consideration.

Taxonomy and material. The genus *Bactrynium* was erected by Emmrich in 1855 for a 'Problematicum' from the Kössener Schichten (Rhaetian) of Austria. *Pterophloios* Gümbel 1861 is a junior synonym. The structure of *Bactrynium* was first clearly described by Zugmayer (1880), who emphasized its similarities to '*Thecidea*', i.e., in modern terms, to the Thecideacea. At the same time Zugmayer erected the genus *Thecospira* for small Triassic shells that had previously been assigned to '*Thecidea*', but in which he discovered a spiral brachidium of a unique kind.

For some time *Thecospira* was commonly regarded as a spiriferide, purely on account of its brachidium, but Williams (1953a) showed that in all other respects it is clearly related to the Strophomenida, and in the *Treatise* (Williams 1965) it is placed in a monotypic family Thecospiridae within the Davidsoniacea.

The affinities of *Bactrynium* have remained more controversial. Waagen (1883) and Bittner (1890) agreed that it differed from '*Thecidea*' and either represented a transition from *Oldhamina* and related genera (i.e. Lyttoniacea) or else belonged to that group. In their studies of Permian Lyttoniacea from Timor, Broili (1916) and Wanner (1935) concurred in this judgement; but, on the other hand, Noetling (1905) and Kozlowski (1929) argued that its similarities to the lyttoniaceans were the result of convergence. The former view has been maintained more recently by Stehli (1956); and the latter by Sarycheva (1964), and also by Makridin (1960) in the *Osnovy* (where *Bactrynium* appears under the name *Pterophloios* in the Thecideacea). In the *Treatise*, on the other hand, it is given a monotypic family Bactryniidae, which is placed provisionally among the Lyttoniacea (Williams 1965).

Bactrynium is known only from the Rhaetian of Austria. Its rarity is such that many features of the morphology remain as obscure as they were in Zugmayer's day. Nevertheless enough can be determined from the available specimens to make a functional reconstruction feasible. I have re-examined Zugmayer's original specimens of the type species *B. bicarinatum* (Emmrich), which are now in the Paläontologisches Institut der Universität, Vienna (PIUW), together with others in the Naturhistorisches Museum, Vienna (NHMW), the U.S. National Museum, Washington (USNM), and the British Museum (Natural History), London (BMNH).

Thecospira is less rare, but is never a common fossil. It has a wider stratigraphical range, from Karnian to Rhaetian, but is confined to the East Alpine region. The best specimens are from the Raibl and St. Cassian beds (Karnian) of the Italian Alps, and from the Kössener and Starhemberger Schichten (Rhaetian) of Austria. I have re-examined Zugmayer's original specimens of the type species *T. haidingeri* (Suess), together with other specimens of that and other species, in the museums already listed. I have also collected *Thecospira* from the St. Cassian beds near Cortina d'Ampezzo; these specimens are now in the Sedgwick Museum, Cambridge (SM).

GENERAL FUNCTIONAL MORPHOLOGY

Relation to substratum. Both *Thecospira* and *Bactrynium* are small brachiopods, the largest dimension of the shell being generally less than a centimetre. Both have a roughly elliptical commissure plan, the major axis being transverse in *Thecospira* and longitudinal in *Bactrynium*. In the latter, the commissure may also have a pair of postero-lateral horizontal deflections (cf. Rudwick 1959, p. 10) which produced corresponding ear-like extensions of the valves themselves. The ventral valve of both brachiopods is strongly and fairly uniformly convex. The dorsal valve of *Thecospira* is weakly convex near the umbo, becoming plane and then weakly concave towards the commissure: in other words the convexity was reversed gradually during ontogeny. The dorsal valve of *Bactrynium* is more strongly concave; available specimens do not show clearly whether it too passed through a convex stage early in ontogeny.

The terms *dorsal valve* and *ventral valve* are used throughout this paper, because *brachial valve* and *pedicle valve* are, in my opinion, misleading and inappropriate: in living articulates neither the brachia nor the pedicle 'belong' to one valve more than the other, in embryonic origin or in adult anatomy; and in many fossil articulates no pedicle existed and there is no direct evidence of the brachia.

There is no trace of a pedicle foramen in either brachiopod, but there is a prominent cicatrix ('scar') of attachment at the apex of the ventral valve. Its appearance suggests that the young shells were generally cemented to shell fragments. The size of the cicatrix shows that when the ventral valve had grown to some 2–4 mm. in breadth its edge began to grow away from the surface of attachment, with consequent increase in the convexity of the valve. Concurrently, at least in *Thecospira*, the dorsal valve became plane and then concave. The orientation of the cicatrix in larger specimens, and its size relative to the whole shell, make it unlikely that the cementation attachment remained effective throughout life. The enclosing argillaceous sediments suggest that apart from scattered shell fragments the substratum was probably soft and muddy. As they grew in size, both brachiopods probably outgrew the shell-fragments on which the spat had settled, and gradually 'heeled over' until they lay freely on the ventral valve, resting on or partly in the soft substratum (text-figs. 8, 10). The ever-increasing convexity of the ventral valve could have ensured that the commissure remained above the surface throughout. A similar relation to the substratum, with an attached stage gradually superseded by a free-lying stage, has probably been common in several brachiopod groups with concavo-convex shells (Rudwick 1965, p. H203; Grant 1966).

Hinge and musculature. There is a moderately broad strophic hinge-line in *Thecospira*. Growth on the hinge-line sectors of the valves produced broad plane interareas on both valves, that on the dorsal valve being very low (text-fig. 1A, Pl. 65, figs. 1, 3; Pl. 66, figs. 17, 18; Pl. 68, figs. 12, 13). Contrary to the description in the *Treatise* (Williams 1965), *Bactrynium* is also strophic, with a very broad hinge-line. This is most clearly seen in a specimen of Zugmayer's, where the dorsal valve is bounded posteriorly by a low plane interarea similar to that of *Thecospira* (text-fig. 2A; Pl. 68, fig. 2). Williams (1965)

notes correctly that the ventral valve shows no trace of the 'posterior flap' of shell
material that is characteristic of lyttoniaceans.

In *Thecospira* the pseudodeltidium and chilidium are often precisely flush with the
interareas; the growth-lines on the interareas thus cross the mid-line without deflection
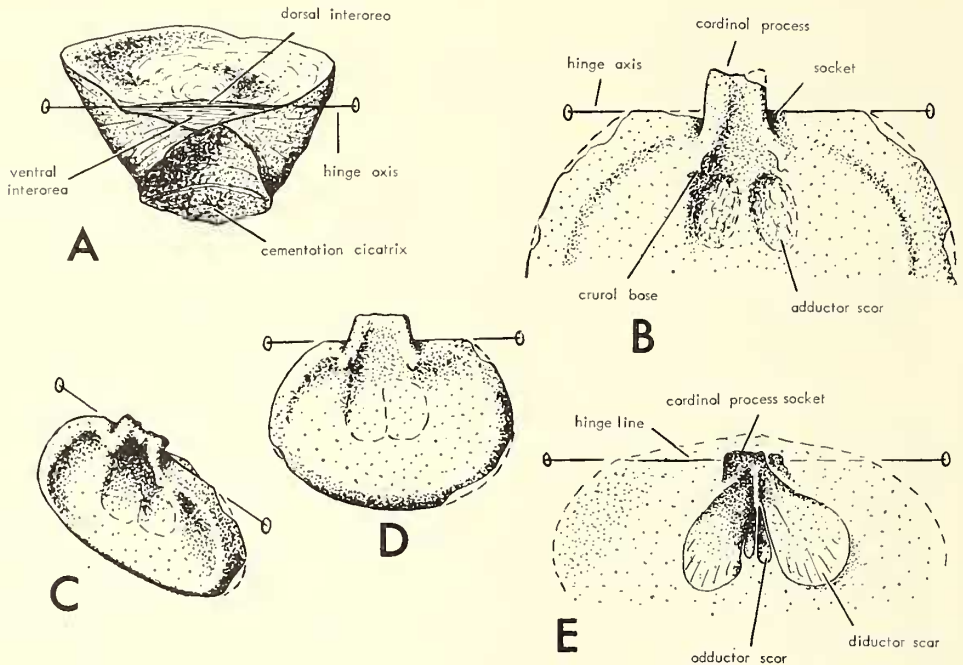
TEXT-FIG. 1. Drawings of *Thecospira*, to illustrate morphology.
A. Postero-dorsal view of *T. haidingeri* (Suess), ×4 (specimen as in Pl. 65, figs. 1–4).
B. Ventral view of dorsal valve of *T. tyrolensis* (Loretz), ×4 (specimen as in Pl. 65, figs. 12, 13).
C. D. Oblique and ventral views of dorsal valve of *T. haidingeri*, ×4·5 (specimen as in Pl. 65, figs. 8,9.)
E. Dorsal view of ventral valve of *T. haidingeri*, ×4·5 (specimen as in Pl. 65, fig. 7).

(text-fig. 1A; Pl. 65, fig. 1; Pl. 66, figs. 17, 18). In some shells the pseudodeltidium is
more clearly delimited (Pl. 68, figs. 11, 12); and there are other Triassic shells originally
described as 'Thecidea', which may in fact be *Thecospira* or closely related to it, in which
the pseudodeltidium is slightly but distinctly convex (Pl. 68, fig. 13).

EXPLANATION OF PLATE 65

Figs. 1–11. *Thecospira haidingeri* (Suess), Rhaetian, Austria. 1–4, Dorsal, ventral, posterior and left
lateral views of whole shell ×3 (PIUW; figured Zugmayer 1880, pl. 2, fig. 33), from Kitzberg.
5–6, Details of ventral and dorsal valve surfaces of same specimen ×9. 7, Interior of ventral valve
×3 (PIUW; figured Zugmayer 1880, pl. 2, fig. 35), from Kitzberg. 8–9, Ventral and oblique pos-
terior views of interior of dorsal valve ×3 (PIUW; figured Zugmayer 1880, pl. 2, fig. 36), from
Dürnbach. 10–11, Ventral and oblique posterior views of spiral brachidium in dorsal valve, exposed
by grinding and polishing ×9 (PIUW; figured Zugmayer 1880, pl. 2, fig. 39), locality unknown.
J, jugum; C, crus. 12–13, *Thecospira tyrolensis* (Loretz), Raibler Schichten, Romerlo, near Cortina
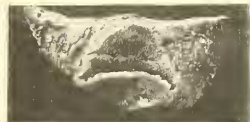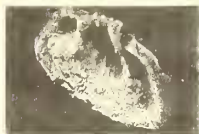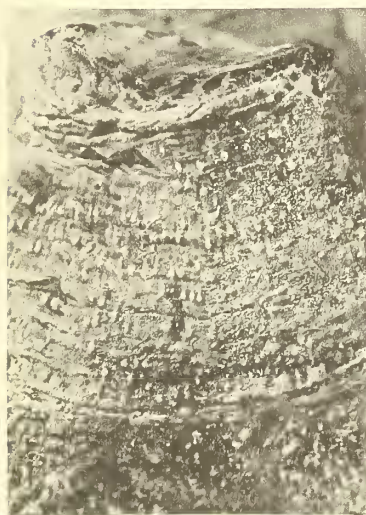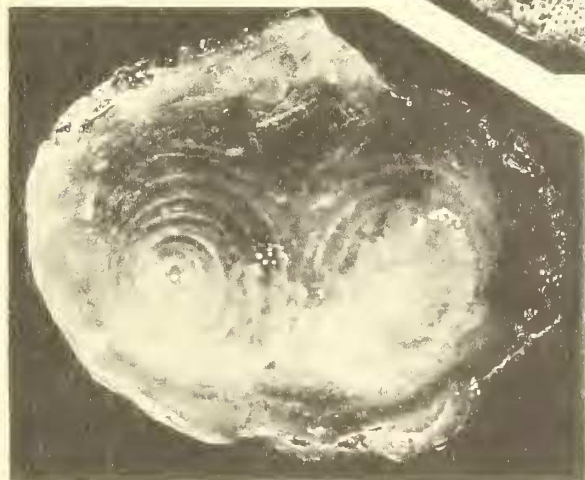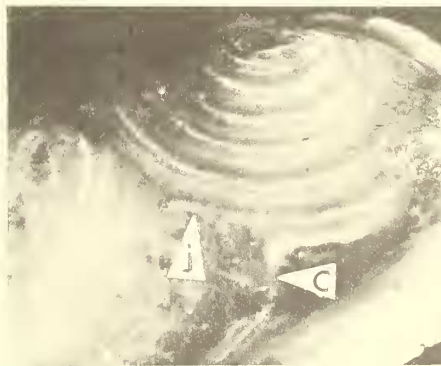d'Ampezzo, Italy. Ventral and oblique posterior views of interior of dorsal valve ×3 (NHMW).
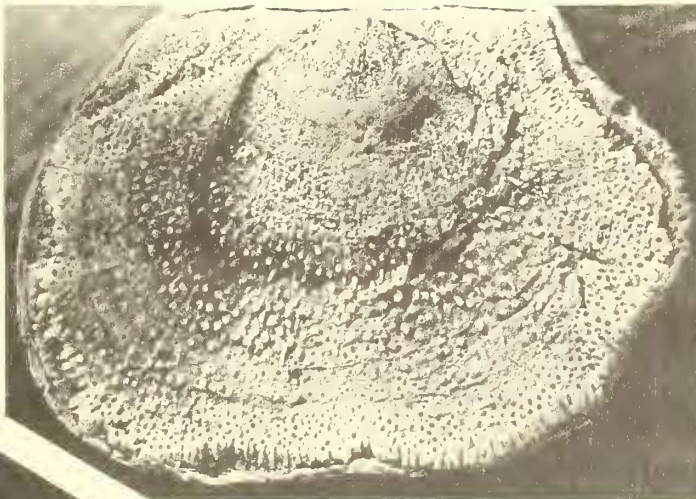
The form of the pseudodeltidium and chilidium in *Bactrynium* are not known with certainty. The fragmentary dorsal valve already referred to is not well enough preserved to show the chilidium clearly, though it was probably convex and arched over the base of the cardinal process. '*Thecidea bicarinata*' Klipstein, which may be congeneric, has a convex pseudodeltidium and chilidium.

Thecospira has a pair of strong teeth, unsupported by dental lamellae, projecting forwards from beneath the pseudodeltidium (Pl. 68, fig. 11). The corresponding sockets are defined medially by the sides of the large rectangular cardinal process, and anteriorly by 'socket plates', which are simply low ridges formed by the sides of the cardinal
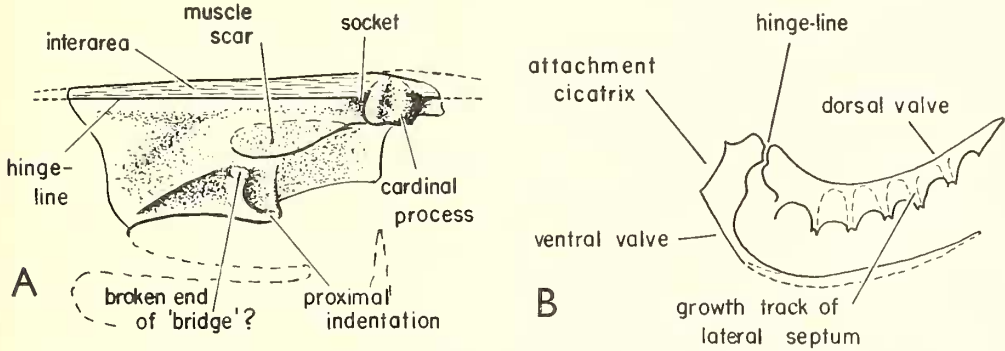
TEXT-FIG. 2. Morphology of *Bactrynium*.

A. Postero-ventral view of fragment of dorsal valve, showing strophic hinge and low interarea, cardinalia, muscle scar, and posterior region of 'lobate apparatus', × 10 (specimen as in Pl. 68, fig. 1, 2).
B. Longitudinal section through shell, showing concavo-convex form, with growth tracks of lateral septa, × 5 (specimen as in Pl. 68, fig. 9).

process curving antero-laterally to merge with the floor of the valve (text-fig. 1B–D; Pl. 65, figs. 8, 9, 12, 13; Pl. 66, fig. 16). The teeth of *Bactrynium* are not yet known, but the cardinalia in the dorsal valve are very similar to those of *Thecospira*, though the cardinal process is relatively smaller (text-fig. 2A; Pl. 68, fig. 1, 2). These hinge structures are in no way abnormal.

The degree of rotation possible with this articulation cannot easily be inferred. The hinges have some mechanical resemblance to that of the living *Lacazella*, in which the angle of opening approaches 90° (Lacaze-Duthiers 1861). Possibly the shells of *Thecospira* and *Bactrynium* opened to a similar extent. The feeding mechanisms reconstructed in this paper would be feasible with either a small or large angle of opening.

The cardinal process of *Thecospira* is indistinctly bilobed (text-fig. 1B–D; Pl. 65, figs. 8, 9, 12, 13; Pl. 68, fig. 12), and the diductor attachments are visible distally. The cardinal process projects into a deep cavity beneath the pseudodeltidium (Pl. 68, figs. 11, 12). On the floor of the ventral valve the diductor attachments are large and flabellate (text-fig. 1E; Pl. 65, fig. 7). Between them are the narrow lanceolate attachments of the adductors. I have not seen the median septum in the ventral valve mentioned in the *Treatise* description. The adductor scars on the dorsal valve are elliptical, are not divided into anterior and posterior pairs, and are separated in the mid-line by a long narrow ridge (text-fig. 1B–D; Pl. 65, figs. 8, 13; Pl. 66, fig. 16).

The cardinal process of *Bactrynium* is also indistinctly bilobed. Lateral to its base is a smooth transversely elliptical area (text-fig. 2A; Pl. 68, fig. 2), which closely resembles the scar of the 'lateral adductor' muscle in the living *Lacazella* and the similar scars in Jurassic thecideaceans such as *Eudesella* and *Davidsonella* (Pl. 68, figs. 3, 4). No other scars are visible on the dorsal valve, but the preservation is not ideal; the scars on the ventral valve are not known at all.

In *Thecospira* the muscular leverage involved in opening and closing the shell was in no way unusual. The musculature is here reconstructed (text-fig. 8) on the conjectural assumption that the muscles were columnar (as in living thecideaceans and inarticulates) and not tendonous (as in living rhynchonellides and terebratulides). If the adductors were differentiated into striated 'quick' and unstriated 'catch' portions, these portions were not separated spatially like the anterior and posterior adductors of living rhynchonellides and terebratulides. The orientation of the diductors shows that a wide degree of opening of the shell would have been mechanically possible, if allowed by the articulation.

As far as available evidence goes, the muscular leverage of *Bactrynium* was also 'normal', apart from the lateral shift of the main adductors, which is also known in the thecideaceans.

In both brachiopods the soft tissues would have been sealed extremely effectively and strongly when the shell was closed, for the lid-like dorsal valve has a strongly thickened submarginal rim (text-fig. 1B–D; Pl. 65, figs. 8, 9, 12, 13).

'*Ornament*' *and shell structure.* Primary-layer shell covers the exterior of both valves in the normal way. In *Bactrynium* it is marked only with finely wrinkled growth-lines (cf. Bittner 1890, pl. 26, fig. 18). In *Thecospira* there are small tear-shaped pustules, oriented radially and apparently scattered over the entire shell surface (Pl. 65, figs. 5, 6). Where best preserved, they appear to have been short slender spinelets (Pl. 65, fig. 6, central area of dorsal valve); and among them are faint traces of radial costellae (Pl. 65, fig. 6, umbonal region). Some shells from the Cortina area have fewer pustules and much more conspicuous radial costellae, with new costellae added by intercalation (Pl. 68, fig. 12). There are no large tubular spines of productoid type on either brachiopod.

A detailed study of shell structure is beyond the scope of this paper, but the known structures must be mentioned briefly in view of their prominence in discussions on affinity. *Bactrynium* is said to be pseudopunctate (Williams 1965), and this seems to be

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confirmed by a study of Zugmayer's original sections, though these are crude by modern standards. The structure of *Thecospira* is more problematical. Suess noted in his original description of *T. haidingeri* that it was punctate (1854, p. 44), and this is very clearly shown by Zugmayer's specimens (Pl. 65, figs. 5, 6). But Bittner (1890) commented that although some species are punctate, others are apparently impunctate. Cellulose peels taken from several specimens confirm that there is a genuine diversity of shell structure within the genus. This must clearly be taken into account in any future systematic revision; for the present, it is sufficient to outline the nature of the diversity.
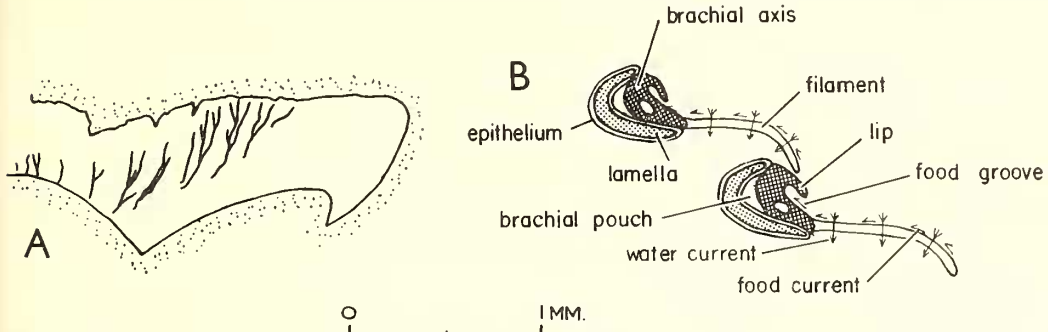
TEXT-FIG. 3. Morphology of *Thecospira*.

A. Diagram based on a polished longitudinal section through a dorsal valve of *Thecospira* sp., showing punctae coalescing as they traverse the shell; external surface above. More punctae are shown than actually lie in the plane of the section; since they are picked out by matrix they are visible for a further part of their course. St. Cassianer Schichten, Alpe di Specie, near Cortina d'Ampezzo, Italy; SM.G.1260.

B. Reconstruction of brachium of *Thecospira*: cross-sections of two adjacent whorls, with filaments in inferred natural orientation; for further explanation see text.

Specimens of *Thecospira* sp., from the St. Cassian beds of the Alpe di Specie [Seelandalpe], near Cortina, are punctate, but the punctation is most unusual. Closely spaced, thick punctae of the exterior shell layers coalesce into comparatively few, more widely spaced punctae as they cross the shell thickness (text-fig. 3A). Probably the structure is the same as that described loosely by Bittner in *Thecospira davidsoni* (1890, p. 287). Similar types of punctation are known elsewhere in the phyl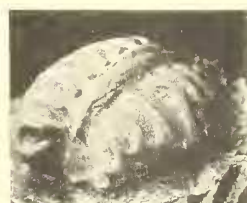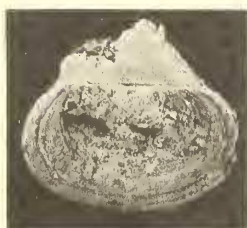um only in some inarticulate brachiopods (e.g. *Crania*) and in the Silurian enteletacean *Dicoelosia* (Wright 1966); but all three occurrences of this type of punctation are likely to represent independent developments of the structure.

T. tyrolensis (Loretz) is impunctate, but the shell structure appears complex because of the presence of small pimples or pustules on the inner surface of the valves. As shell growth proceeds, the pustules are incorporated in the secondary shell layer. *T. guembeli* (Pichler), on the other hand, has a shell structure which can be regarded as obscurely pseudopunctate; there is a 'normal' primary and secondary-layer structure with an inner layer in which the orientation of the crystals is irregular.

Coelom and body wall. In living articulates the coelom, bounded by the body wall and containing the muscles, gut, etc., is confined to a small postero-median part of the shell cavity. The body-wall is 'wrapped' closely round the anterior and lateral surfaces of the

muscles, and laterally it incorporates the crura. A consistent reconstruction of the body wall of *Thecospira* can be made by homology. The crura or 'apophyses' project forwards from the 'socket plates' at the base of the cardinal process, in a position consistent with a body-wall wrapped around the lateral surfaces of the muscles (text-figs. 1B–D, 8, 9).

A reconstruction of the gut, though given here for the sake of completeness, is necessarily conjectural. Its position and form as shown (text-fig. 9) are, however, consistent with what is known of living articulates. An enlarged stomach and lateral digestive glands would have fitted neatly into the space (otherwise empty) behind the adductors
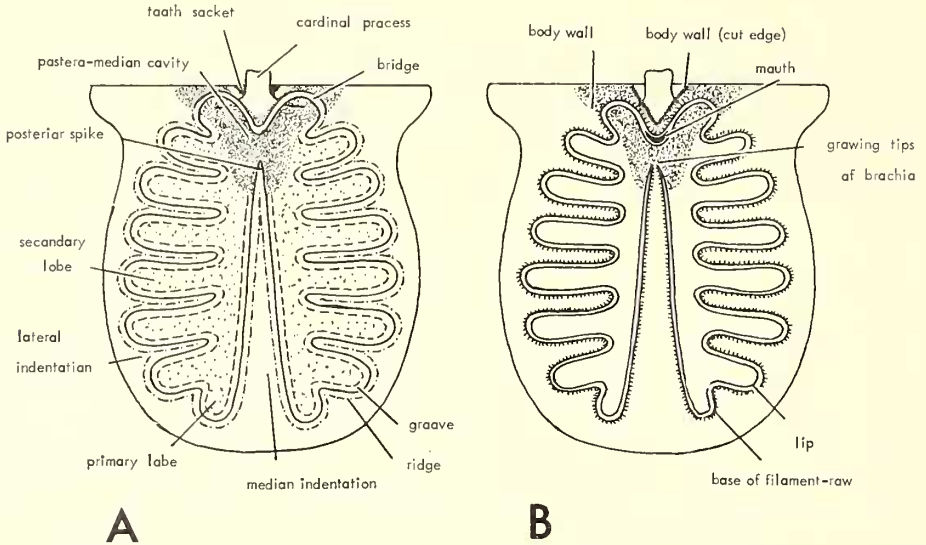
TEXT-FIG. 4. Diagrams to show (A) morphology of 'lobate apparatus' on dorsal valve of *Bactrynium*, and (B) its interpretation as a supporting structure for a complex ptycholophous lophophore.

and above the diductors, occupying also the concavity at the base of the cardinal process (text-fig. 1B–D; Pl. 65, figs. 9, 13; Pl. 66, fig. 16).

When the shell of *Bactrynium* is preserved closed there is little space between the ridged internal surface of the dorsal valve and the corresponding surface of the ventral valve. Posteriorly, however, the dorsal valve is 'excavated' (strictly speaking, it is not thickened like the rest of the valve) into a broad median cavity (text-fig. 4A; Pl. 66, figs. 2, 10). There is a similar cavity in thecideaceans (Pl. 66, fig. 15), and in the living *Lacazella* this is known to accommodate the dorsal part of the 'body' (coelom) with viscera and muscles. It is, therefore, reasonable to infer that the 'body' of *Bactrynium*, like that of *Thecospira*, was confined to a small median-posterior portion of the shell cavity (text-fig. 4B).

THE LOPHOPHORE

The brachidium in Thecospira. The spiral brachidium of *Thecospira* consists of a pair of low conical spiralia, attached to the dorsal valve by a pair of crura or 'apophyses', and linked to each other proximally, across the median plane, by a simple jugum.

The crura are short peg-like processes, circular in cross-section, which project forwards from the 'socket plates' near the base of the cardinal process. In most specimens they are broken off, and their position is only shown by a pair of small residual tubercles on the 'socket plates' (text-fig. 1B–D; Pl. 65, figs. 9, 12). Their connexion with the spiralia is, however, visible on Zugmayer's ground and polished specimen (Pl. 65, fig. 11). The crura manifestly had the same function as the crura of other brachiopods, and they project from the cardinalia in essentially the same way; therefore it seems hardly necessary to distinguish them by another term ('apophyses', cf. Williams 1965). The differences, which are part of the evidence for regarding the brachidium of *Thecospira* as a separate development, are in the cardinalia rather than the crura themselves.

The spiral axis of each spiralium is inclined, with the apex of the spiral pointing latero-ventrally. The spiralia occupy almost the whole of the shell cavity, and when the shell is closed the spiral lamellae lie very close to the internal surface of the ventral valve (cf. Bittner 1890, text-fig., p. 310). The lamella is unique, as Zugmayer emphasized, by being U-shaped in cross-section. No such gutter-like lamella is known in any of the Spiriferida. The gutter faces outwards around the spiral (Pl. 65, figs. 10, 11). The ventral limb of the 'U' is narrower than the dorsal. The ventral side passes proximally into the jugum, the dorsal into the crura. The structure of the jugum is not very clear in Zugmayer's specimens, and it has not been detected with certainty in serial cellulose peels. Possibly it consists only of crural processes, projecting towards the mid-line without meeting each other (Pl. 65, fig. 11).

Lobate apparatus of Bactrynium. On the internal surface of the dorsal valve of *Bactrynium* there is a series of lobed ridges and grooves. This 'lobate apparatus' is approximately, but not accurately, symmetrical about the median plane. It consists of a pair of longitudinally elongated *primary lobes* separated by a long *median indentation*, and up to ten pairs of laterally elongated *secondary lobes* projecting laterally from the primary lobes and separated from one another by *lateral indentations* (text-fig. 4A). An occasional *tertiary lobe* branches from a secondary lobe as a minor irregularity (text-fig. 5B, lobe 5 left). The lobes have sub-parallel sides, and approximate to a uniform width of about 0·9 mm. in all parts of all specimens (text-fig. 5). The lateral indentations likewise have sub-parallel sides, and approximate to a uniform width of about 0·3 mm. The median indentation has a similar width posteriorly, but broadens anteriorly. (The uniform width of the lobes and indentations is partly obscured in text-fig. 5 by the foreshortening of the peripheral parts, due to the strong convexity of the internal surface of the valve.)

The lobes and indentations are outlined by the sinuous course of a closely contiguous groove and ridge (text-fig. 4A). These can be seen with variable clarity in different specimens; this is partly due to differences of preservation, but there may be some genuine variation. The groove is internal in position, the ridge external. The steep slope between them is always clearest: the course of this outer edge of the groove (or inner edge of the ridge) is shown by a continuous line in text-figs. 4A and 5, and is the basis of the measurements given above.

The ridge is clearly visible, and clearly raised above the rest of the valve surface, in the broad anterior part of the median indentation (Pl. 66, figs. 1, 2, 5–7, 10). In the narrower posterior part the ridges of the left and right sides generally coalesce into

a single ridge; but in the best-preserved specimens the median indentation is clearly 'double' right to its tip (Pl. 67, fig. 5; Pl. 68, fig. 1). The posterior tip of the median indentation projects as a conspicuous *spike* overhanging the postero-median cavity (Pl. 66, figs. 1, 10): this spike is vulnerable to damage and has generally been broken off at its base. As in the median indentation, the ridges on either side of each lateral
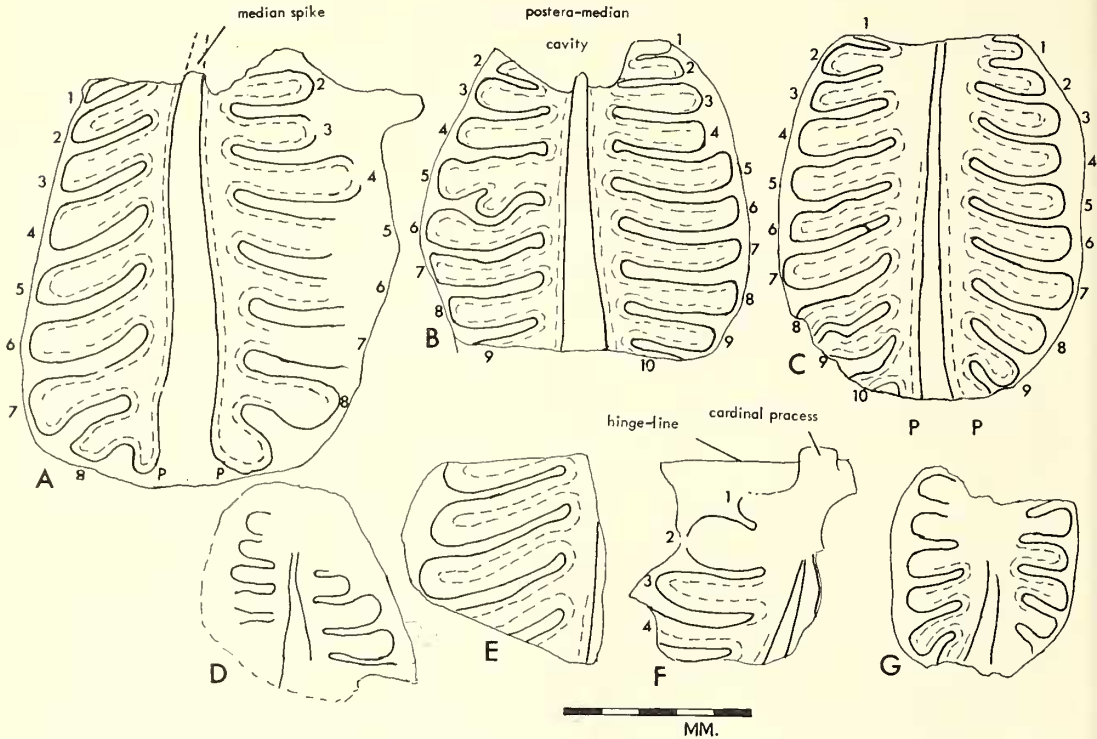
TEXT-FIG. 5. Drawings of the 'lobate apparatus' on dorsal valves of *Bactrynium*, to show uniformity of dimensions of lobes and indentations, all ×5. Continuous line indicates slope between groove and ridge; dashed line, inner edge of groove. (Details of specimens given in captions to plates: A, as Pl. 66, figs. 1, 2; B, as Pl. 66, figs. 9–12; C, as Pl. 66, figs. 5–7; D, as Pl. 67, fig. 7; E, as Pl. 67, fig. 4; F, as Pl. 66, fig. 8; G, as Pl. 67, fig. 3.) Scale represents 5 mm.

EXPLANATION OF PLATE 67

Figs. 1–8. *Bactrynium bicarinatum* Emmrich, from the Kössener Schichten of Austria. All figures ×6; figs. 1–4, 7–8 are whitened with ammonium chloride.

1, 2, Internal surface of dorsal valves, enlarged from Pl. 66, figs. 1 and 5 respectively, to show lobed groove and pustular area within groove. 3, Internal surface of dorsal valve of small (young?) specimen from Kössen, to show smaller number but similar dimensions of lobes (PIUW; figured Zugmayer 1880, pl. 2, fig. 17). 4, Internal surface of fragment of dorsal valve from Kitzberg, to show pustular area within groove (PIUW; figured Zugmayer 1880, pl. 2, fig. 20). 5, Internal surface of dorsal valve, enlarged from Pl. 66, fig. 10, to show postero-median cavity and minor irregularities in lateral lobes. 6, Dorsal valve ground down to show lateral indentations, median spike, and posterior bridge (PIUW; Zugmayer coll.; specimen coated with oil before photographing). 7, Internal surface of dorsal valve of small (young?) specimen from Kössen; compare with fig. 3 (BMNH B.2103). 8, Internal surface of dorsal valve, enlarged from Pl. 66, fig. 13.

PLATE 67
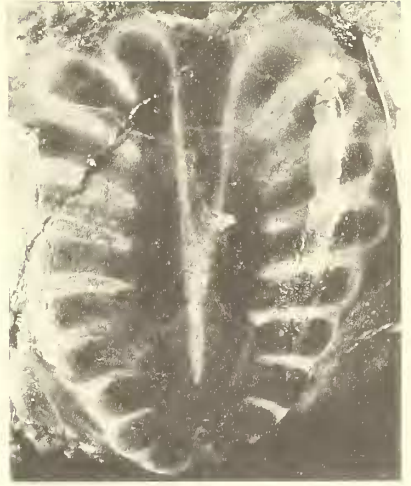
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indentation are often coalesced into a single ridge or 'lateral septum'; but here too the best specimens show that the ridge is double in origin (Pl. 67, fig. 4; Pl. 68, fig. 1). Around the distal end of each lobe the ridge may be clearly marked or may merge insensibly into the peripheral part of the valve surface.
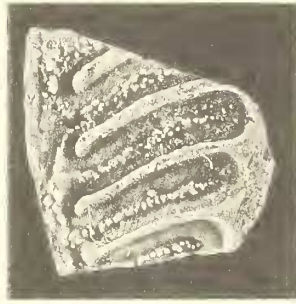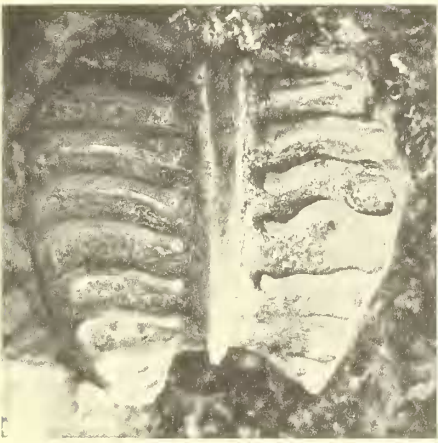
The groove likewise is variably expressed; it may be clearly differentiated from the central area of the lobes or may merge insensibly into it. Where the inner edge of the groove is distinct, it is shown by a dashed line in text-fig. 5. The central area of the lobes is differentiated, at least in the best specimens, by a distinctly pustular surface (Pl. 67, figs. 2–5).

The posterior extremity of the groove/ridge structure is not entirely clear. The most posterior pair of secondary lobes are generally short, and lie antero-lateral to the cardinal process. At first sight it might appear that the groove runs into the base of the cardinal process (Pl. 66, figs. 3, 8, 11; cf. Williams 1965, p. H521). But this is an illusion. A specimen of Zugmayer's, ground down to expose the ridges, shows clearly that the ridges of left and right sides fused with one another in the median plane to form a forwardly projecting V-shaped structure (Pl. 67, fig. 6). Zugmayer himself referred to this as a *bridge*, and this interpretation appears to me to be correct. In other words, at points antero-lateral to the cardinal process the ridge rises away from the floor of the valve and crosses the postero-median cavity as a bridge-like lamella (text-fig. 4A). In the best-preserved specimens (Pl. 66, fig. 3; Pl. 68, fig. 1) the ridges appear to end abruptly, but these are evidently breakage surfaces at the points where the ridges became a free lamella. It is clearly distinct from the 'socket plate' running into the base of the cardinal process (text-fig. 2A).

Brachial axis of Thecospira. The entire brachidium of *Thecospira*, like that of any other articulate, is clearly an outgrowth of the secondary-layer material of the dorsal valve. As such, it must have been sheathed by, and secreted by, an extension of the outer mantle epithelium (cf. Williams 1956). As with the spiral brachidia of spiriferides, geometrical considerations alone are sufficient to prove that this epithelium must have had the power of resorption as well as secretion, or else the brachidium could not have grown in size while retaining its form and relative position.

In their reconstruction of the lophophore of spiriferides, Williams and Wright (1961) make the assumption that the growing tips of the brachia necessarily remained together in the mid-line, on the jugum, throughout ontogeny. But this assumption is not fully supported even by their cited analogy of plectolophes in living brachiopods; in *Gryphus vitreus*, for example, the growing tips are far apart from one another at the distal end of the median coil. Even supposing that a complete jugum was present in *Thecospira*, therefore, I see no justification for reconstructing a 'deuterolophe' (i.e. doubled brachial axes) on the spiral lamellae. The simpler reconstruction of an ordinary spirolophe seems to me more plausible, in view of the close resemblance between the form of the spiral brachidium and that of the spiral lophophores of living rhynchonellides.

On this reconstruction each whorl of the lamellae would have borne a corresponding single whorl of the brachial axis, and the growing tips of the brachia were at the tips of the lamellae. As suggested previously (Rudwick 1960, text-fig. 6D), the brachial axis is shown, conjecturally, nestling within the 'gutter'; if this is correct the filament-row, at least near its base, would have projected outwards around each whorl. If the lophophore

was supported throughout its length by the brachidium, the great brachial canal, which in most living articulates acts as a hydrostatic skeleton, may have been vestigial or absent; and it is so shown, conjecturally, in the reconstruction given here (text-fig. 3B).

Proximally, by homology with living brachiopods, the axis would have continued towards the mid-line, lying adjacent to the crural processes or jugum. The mouth would have been situated in the mid-line. At this point, if the basic orientation of the lophophore was like that of all living brachiopods, the filament-row must have been on the posterior or ventral side of the mouth and food-groove, and the lip on the anterior or dorsal side. Then, by tracing the axis laterally on to the spirals, it follows by simple topology that the filament-row must have been on the *dorsal* side of the food-groove, and the lip on the ventral, on each of the outwardly facing whorls of the spirolophe. The brachial axis is similarly twisted in the proximal parts of the spirolophes and plectolophes of living brachiopods (Rudwick 1962, text-figs. 7c, 9c, 12b).

Brachial axis of Bactrynium. The mode of growth of the lobate apparatus can be inferred quite simply (text-fig. 6). A section of Zugmayer's, cut longitudinally through the dorsal valve parallel to the median plane, shows clearly that the lobate apparatus grew by simple accretion. The 'lateral septa' (i.e. the coalesced doubled ridges in the lateral indentations) remained in the same absolute position during the growth of the valve, for their growth tracks can be seen projecting through the thickness of the valve perpendicular to its outer surface (text-fig. 2B; Pl. 68, fig. 9). Since the valve grew not only in thickness but also in area, any given lobe must therefore have changed in *relative* position during ontogeny, becoming progressively more posterior. The distal ends of the lobes are near the valve edge in specimens of all sizes: therefore the lobes must have grown in

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EXPLANATION OF PLATE 68

Bactryuium, Thecospira and other brachiopods for comparison. All figures × 6. All except fig. 9 whitened with ammonium chloride.

Figs. 1, 2. *Bactryuium bicariuatum* Emmrich; ventral and posterior views of fragment of dorsal valve; see also text-fig. 2A. Kössener Schichten of Dürnbach (PIUW; figured Zugmayer 1880, pl. 2, fig. 18).

Fig. 3. *Eudesella mayalis* (Deslongchamps), from the 'Couche à Leptaena' (Upper Lias), of May, Calvados, France; interior of dorsal valve (SM.F.20273).

Figs. 4, 5. *Davidsouella siuuata* (Deslongchamps), from the same locality and horizon; postero-ventral and ventral views of dorsal valve (SM.F.20199).

Fig. 6. *Moorelliua leptaeuoides* (Deslongchamps), from the same locality and horizon; interior of dorsal valve (SM.F.20258).

Figs. 7, 8. *Elliottiua deslougchampsi* (Davidson), from the Middle Lias of May, Calvados, France; ventral and postero-ventral views of dorsal valve (SM.F.20288).

Fig. 9. *Bactryuium bicariuatum* Emmrich, longitudinal section of dorsal valve (and part of ventral), showing growth tracks of lateral septa; see also text-fig. 2B. (PIUW; figured Zugmayer 1880, pl. 2, fig. 32.) Locality unknown.

Fig. 10. *Lyttonia* sp., internal surface of part of dorsal valve, for comparison with *Bactryuium*. Sandy limestone beds above Middle Productus Limestone (Permian), Banschang, East of Chideru, Salt Range, Pakistan (Yale University, Peabody Museum, 22954).

Figs. 11, 12. *Thecospira* sp. Dorsal views of ventral valve alone and of both valves as found in loose association, to show pseudodeltidium, articulation and radial costellae. Raibler Schichten, Rumerlo, near Cortina d'Ampezzo, Italy (R. Zardini coll.).

Fig. 13. '*Thecidea* sp.' (*Thecospira*?), dorsal view of shell, to show convex pseudodeltidium, from Helenenthal, Baden (PIUW; figured Zugmayer 1880, pl. 2, fig. 41).

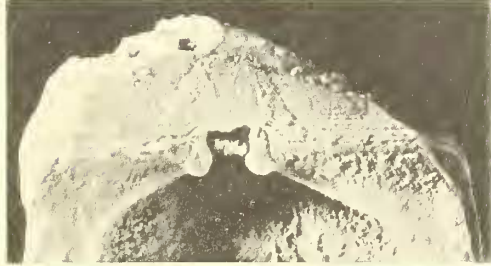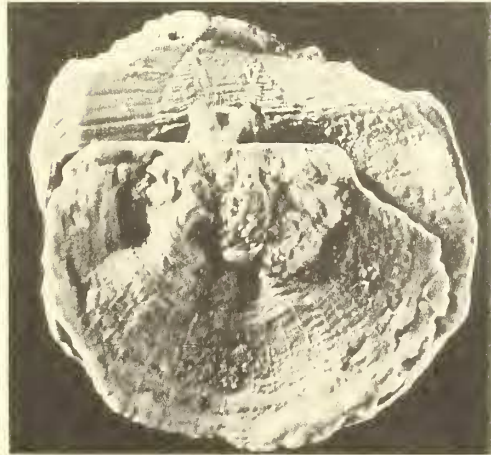length during ontogeny, extending laterally as the valve increased in breadth. At the same time the valve was also growing in length, and therefore the most anterior secondary lobe must have become progressively further from the anterior edge of the valve. But the most anterior secondary lobes, and the primary lobes themselves, are near the anterior edge in specimens of all sizes: therefore new secondary lobes must have been
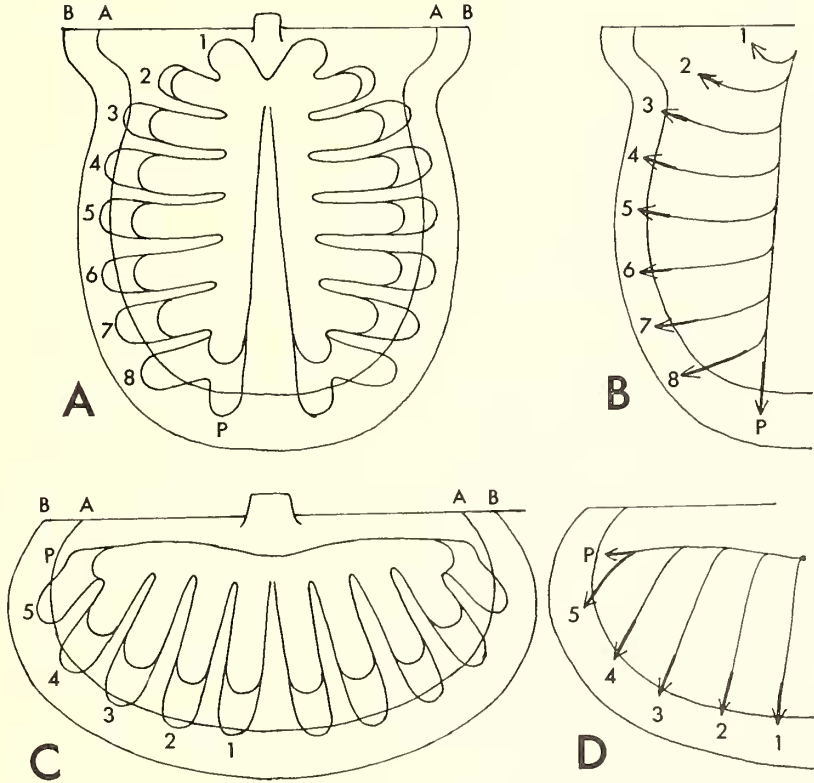
TEXT-FIG. 6. Diagrams to show inferred mode of growth of 'lobate apparatus' of *Bactrynium* (A, B), compared with *Thecidiopsis* (C, D). Figs. A, C show course of lobed groove and ridge; figs. B, D show corresponding growth tracks of axes of lobes; lobes are numbered consecutively in order of derivation from the persistent primary lobes P. As dorsal valve grows in size from AA to BB, lobes grow in length but do not change in absolute position; new lobes (no. 8 in fig. A, no. 5 in fig. C) are budded off from persistent primary lobes.

budded off at intervals during ontogeny from the pair of persistent primary lobes. Thus in text-fig. 6A, during growth of the valve margin from AA to BB, secondary lobes 1 to 7 extended laterally while remaining in the same absolute position on the valve, while the primary lobe extended forwards and budded off the new secondary lobe 8. The whole process of growth of the lobate apparatus could have been achieved simply by differential rates of secretion of shell material over the surface of the valve as it increased in thickness and over-all size: there is no need to postulate any shell resorption (except possibly on the posterior edge of the 'bridge').

This analysis of growth justifies the terminology so far used in a purely descriptive sense. The primary lobe may be so called because it must have persisted throughout ontogeny in a submedian position, growing progressively forwards. The secondary lobes must all have been derived from the primary lobe by lateral budding, in order from the most posterior lobe forwards. The numbering of the secondary lobes thus corresponds to their order of appearance (text-fig. 6B).

The over-all effect of the growth of the lobate apparatus was to keep the internal surface of the valve fully covered (except in the peripheral zone) with a series of lobes and indentations of a constant standard width, whatever the absolute size and area of the valve.

There is a close analogy between the lobate apparatus of *Bactrynium* and the brachia-bearing grooves and ridges in living Thecideacea. On the inner surface of the dorsal valve there is a lobed groove, two-lobed in *Thecidellina*, four-lobed in *Lacazella* (Elliott 1965, fig. 742, 3a; 744, 2a). On the outer side the groove is separated by a conspicuous slope from an outer ridge, though the latter may not be clearly distinguishable from the peripheral zone of the valve. Postero-laterally the outer ridge extends freely above the postero-median cavity, projecting towards the mid-line, or it may fuse with that projecting from the opposite side to form a complete bridge over the cavity. This bridge is clearly separate from the 'socket plates' and cardinal process. In the median indentation the ridges of left and right sides gradually coalesce and project backwards as a spike overhanging the postero-median cavity. Indeed in *Lacazella* all the 'septa' in the indentations may overhang in this way at their inner ends. Internal to the lobed groove is a second, inner ridge, the so-called 'brachial ridge'; within each lobe this is clearly double in origin, but may be coalesced into a single ridge running along the axis of the lobe. This inner ridge, like the outer, may project freely so as to overhang the postero-median cavity. Its crest is often distinctly pustular.

Although the anatomy of living thecideaceans remains imperfectly known in many respects, it is at least clear that the brachial axis of the lophophore is attached throughout its length to the dorsal mantle, and that it lies in the lobed *groove*. This can be seen in both *Thecidellina* (cf. Elliott 1965, fig. 742, 3a) and in *Lacazella* (Lacaze-Duthiers 1861, pl. 3, fig. 1). The frontal side of the axis, bearing the lip, faces inwards, towards the inner 'brachial' ridge; while the outer side, bearing the filament-row, faces outwards, towards the outer ridge. The distal growing tips of the brachial axis are located close together at the tip of the median indentation (Lacaze-Duthiers 1861, pl. 2, fig. 7). The mouth is located medially, on the anterior side of the bridge over the postero-median cavity. The arrangement of the lobes is such that the lophophore of *Thecidellina* is a schizolophe, while that of *Lacazella* is a simple (four-lobed) ptycholophe. (Williams's and Rowell's (1965, p. H38) novel definition of the trocholophous stage, to include all lophophores in which the filaments are arranged in a single series, seems to me to be unwarranted: lophophore growth stages were originally defined by the arrangement of the brachial axis, and should remain so.)

The brachial axis of *Bactrynium* may be reconstructed in a comparable position, attached to the dorsal mantle and lying in the lobed groove, with the filament-row facing the outer bounding ridge and the lip facing the inner pustular area (text-fig. 7D). Then proximally, at the mouth, the axis would have had the normal orientation, with the filament-row on the posterior or ventral side of the mouth and the lip on the anterior

or dorsal side. Thus the lophophore would have been a complex ptycholophe, with up to twenty or more lobes (text-fig. 4B). It may be assumed that the lophophore would have grown, like those of all living brachiopods, only by the lengthening of the brachial axis and the formation of new filaments at the extreme tip of the brachia, in the median indentation. Any given filament would therefore have shifted continually in its *relative* position during the growth of the lophophore. The growth zones of the lophophore and those of the supporting lobate apparatus were thus entirely distinct from one another.
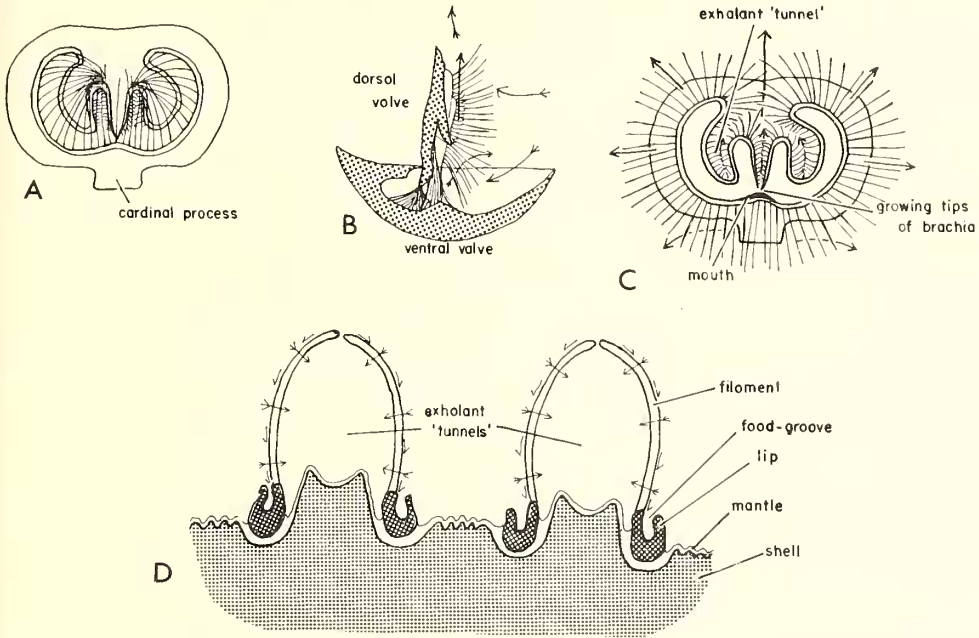
TEXT-FIG. 7. Lophophore and inferred feeding mechanism of *Lacazella* (A–C) and *Bactrynium* (D). A, dorsal valve of *Lacazella* with lophophoral filaments in contracted state, as illustrated by Lacaze-Duthiers (1861, pl. 3, fig. 1); B, C, lophophore of *Lacazella* in inferred feeding orientation, based on Lacaze-Duthier's illustrations of opened shell (1861, pl. 1, figs. 2, 7) and on analogy with *Megathiris* (Atkins 1960); D, reconstruction of brachial axis and filaments of *Bactrynium*, shown as section through two lateral lobes; note brachial axis (dark stippled) in groove in surface of dorsal valve (light stippled), with filaments arching over 'lateral septa' to form 'tunnels'; arrows show water currents and food currents.

FEEDING MECHANISMS

Some elements of the foregoing reconstructions of the lophophore are necessarily conjectural. But of the assumptions made, only three are essential for the validity of the functional interpretation given here: (*a*) that the basic anatomy of the lophophores of *Thecospira* and *Bactrynium* resembled that of all living brachiopods; (*b*) that their basic orientation relative to the body likewise resembled that of all living brachiopods; and (*c*) that in each genus the grooves in the skeletal apparatus bore single rows of the brachial axis, so that the lophophore was spirolophous in *Thecospira* and ptycholophous in *Bactrynium*. For the reconstruction of the feeding mechanisms, i.e. of the lophophores

in operation, one further assumption is necessary: (d) that the basic functional mechanisms of the lophophores were normal, i.e. that they resembled those of all living brachiopods (Rudwick 1962, and references therein). These assumptions of anatomical and physiological uniformity are not of course capable of direct proof. But it is methodologically a sound procedure to begin by testing them indirectly, by determining whether they give a consistent and intelligible explanation of the morphology of the fossils. Only if they fail to do so should departures from uniformity be postulated (cf. Rudwick 1964).

For effective ciliary filter-feeding in a brachiopod, it is essential that the tips of all the filaments (except those projecting at the gape and delimiting the apertures) should touch the mantle surface or the tips of other filaments. Only by so doing can the lophophore divide the mantle cavity into separate inhalant and exhalant chambers and thereby prevent wasteful re-circulation and re-filtering of the water (Rudwick 1960). The possible ways in which a pair of linear brachia can divide the mantle cavity is limited by inherent topological considerations, and only three essentially different arrangements are known in living brachiopods (Rudwick 1962). The spirolophe and ptycholophe, here posulated for *Thecospira* and *Bactrynium* respectively, are two of these three known arrangements.

Current-system of Thecospira. A topological argument developed for the reconstruction of any spirolophe (Rudwick 1960) can be used to infer the attitude of the filaments in *Thecospira*. Inhalant and exhalant chambers could not be isolated unless the filaments on the spiral brachia touched the brachial axis of either the next proximal or the next distal whorl. But on the latter assumption the filaments on the first or most proximal whorl would have touched the axis of the second whorl, and no filaments would have been available to bridge the gap between the axis of the first whorl and the dorsal mantle. Therefore only the former alternative is feasible.

On the distal whorls, the tips of the filaments would thus have touched the brachial axis of the next proximal whorl; on the medial part of the proximal whorl they would have touched either the tips of the corresponding filaments on the other brachium, or else the ventral mantle; anteriorly on this whorl, they would have passed across the gape, projecting freely as apertural filaments; and laterally they would have touched the dorsal mantle. Posteriorly, in the most proximal part of the lophophore, they would have touched the lateral body wall and finally the anterior body wall or ventral mantle (text-figs. 8, 9).

Only by this precise orientation of all the filaments could the spirolophe of *Thecospira* have divided the mantle cavity into separate inhalant and exhalant chambers; by no other arrangement is it topologically possible for this essential functional condition to have been met. Of the only two possible varieties of the spirolophous system, the orientation of the brachidial lamellae thus shows that the interior of the spirals must have been an exhalant space, so that *Thecospira* must have operated the 'exhalant' or '*Spirifer*' type, which has also been inferred for most spiriferides (Rudwick 1960) and is known in the living *Discinisca* (Paine 1962).

The inhalant chamber in *Thecospira* would thus have comprised the ventral part of the mantle cavity, external to the spirals; while the exhalant chamber would have occupied the dorsal part, together with the interior of the spirals, and would also have included a narrow exhalant space between the proximal filaments and the body wall.
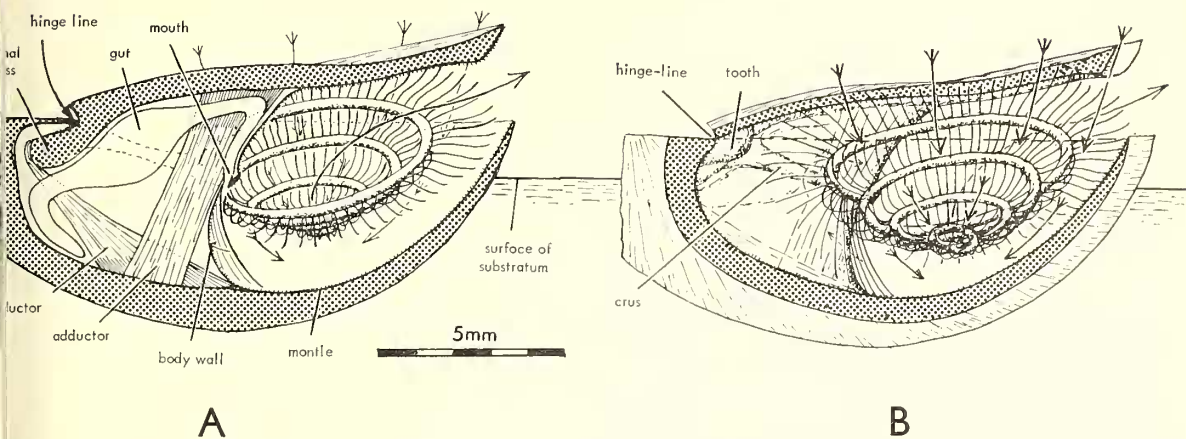
TEXT-FIG. 8. A. Reconstruction of *Thecospira*, lateral view, cut along median plane. Inhalant water (tailed arrows) is seen entering laterally and circulating around exterior of spiral brachium; exhalant water (tailless arrows) is seen emerging from interior of spiral and leaving mantle cavity by a median aperture. To clarify the current system, brachial axes are shown more slender, and filaments more widely spaced, than in reality. Digestive glands omitted.

B. Similar reconstruction, with shell cut in plane parallel to median plane on right side, but with right brachium preserved intact (water currents are those that would operate with whole shell intact); showing crus embedded in lateral body wall, through which muscles and gut are faintly visible. For further explanation see text.

Given this orientation of the filaments, the current system of *Thecospira* follows necessarily (text-figs. 8, 9). Water must have entered the mantle cavity laterally, being drawn down into the inhalant chamber by the pumping action of the filaments removing water into the exhalant chamber. After being filtered between the filaments on the spirals, the water would have flowed as an exhalant current up the axis of each spiral, and then forwards to leave the mantle cavity medially. Water filtered by the most proximal filaments would have flowed along the narrow space between those filaments and the body wall, emerging to join the main exhalant current on either side of the dorsal part of the body wall (text-fig. 9, current 'X'): a similar current can be observed in living articulates (cf. Rudwick 1962, text-figs. 7c, 9a, c, 12b).

Thus the morphology of the brachidium of *Thecospira* is consistent with a ciliary feeding mechanism essentially similar to that of living brachiopods.

The rate at which a lophophore can pump water through a mantle cavity is roughly proportional to the total area of the filament-row. On a spirolophe, the rate is therefore approximately proportional to the area of the roughly conical surfaces which are formed by the spiral brachia when all the filaments are in their natural orientation. Thus in

a spire-bearing brachiopod the larger the conical 'framework' formed by each spiralium, the greater the filtering capacity of the brachium must have been. For a shell of given size, the most effective arrangement of the spiralia would be that which most fully occupies the available space of the mantle cavity, while leaving sufficient space for the circulation of the water currents outside the spirals.
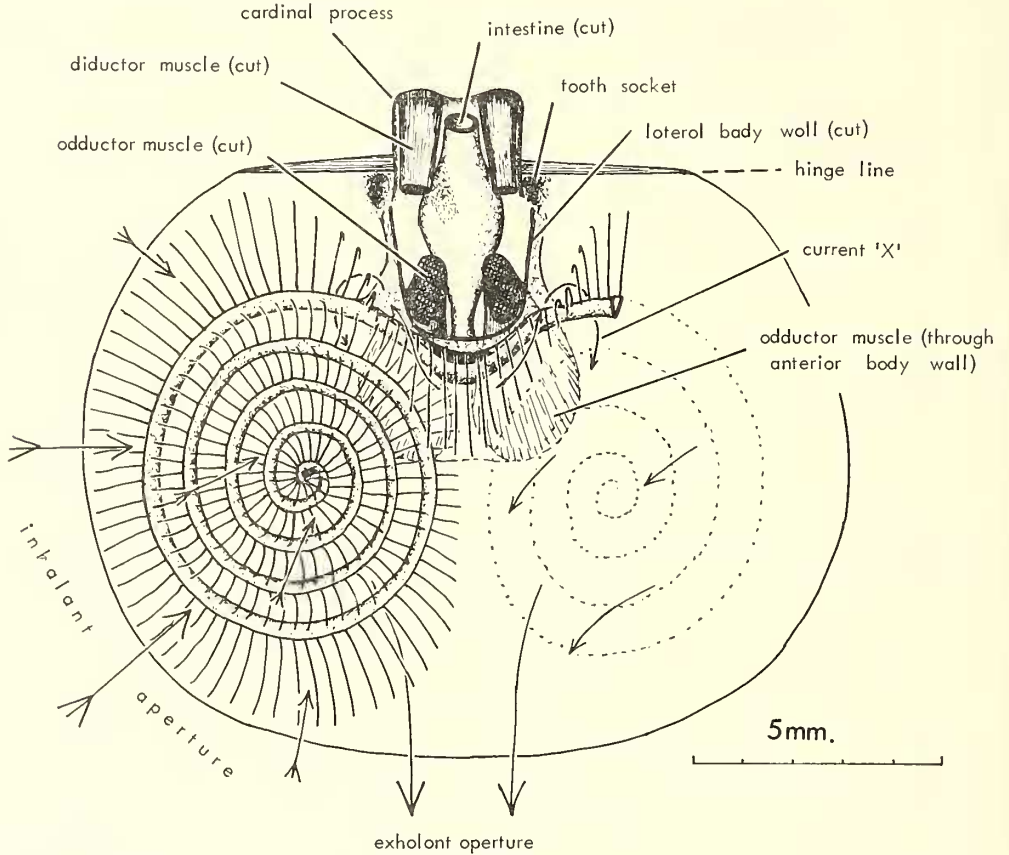
TEXT-FIG. 9. Reconstruction of *Thecospira*, ventral view of dorsal valve, and dorsal part of 'body', with lophophore (right brachium cut off near base to clarify course of exhalant currents). Other conventions as in text-fig. 8.

The observed arrangement of the brachidium in *Thecospira* approximates to this paradigm. The spiralia are so closely moulded to the available space that when the shell was closed the filaments must have been almost or quite in contact with the ventral mantle. When the shell opened, however, the brachidium and lophophore, being attached rigidly to the dorsal valve, would have been raised clear of the ventral mantle, thus allowing the circulation of water outside the spiral brachia.

At the degree of opening selected for illustration here (text-figs. 8, 9), the circulation

space outside the spiral brachia approximates to that observed outside the spirolophes of the living rhynchonellide *Notosaria* and the living *Crania* (Rudwick 1962, text-fig. 7; Atkins and Rudwick 1962, text-fig. 1). If the dorsal valve opened through a wider angle than that shown in this reconstruction, the same current system would have operated, except that the lateral inhalant apertures would have coalesced anteriorly, on the ventral side of the exhalant aperture, to form a single inhalant aperture.

The functional advantage of developing a brachidial support for the spirolophe is not entirely clear. A possible explanation is that a calcareous support for the brachial axis takes up less space than the rather bulky hydrostatic and muscular skeletons seen in the spirolophes of living brachiopods (e.g. Atkins 1963, fig. 8A). Consequently the successive whorls of the spiral brachia can be set more closely together without substantially impeding the flow of water; and thus a greater area of filaments can be accommodated within a mantle cavity of given form and volume. But, on the other hand, this increased efficiency of the lophophore is obtained at the expense of having a supporting structure that is less flexible and more vulnerable to damage than is a hydrostatic skeleton. Thus, a spiral brachidium may on balance be advantageous in some circumstances; but, of course, it is only an available option in those brachiopods that have developed the power of resorption in the epithelia of the mantle.

Current-system of Bactrynium. In a schizolophe or ptycholophe the only effective arrangement of the filaments is for those in the indentations to be flexed abfrontally so that their tips are contiguous. Thus each indentation forms a 'tunnel' of exhalant water, blind-ended proximally but opening peripherally.

Such an orientation is in fact known in all living species in which schizolophes or ptycholophes have been observed in operation. In these lophophores the filaments are flexed abfrontally all along the brachial axis. In a schizolophe the tips of the filaments touch each other across the median indentation, forming a median 'tunnel' which is blind-ended posteriorly but open anteriorly; this has been observed in *Argyrotheca* and *Pumilus* and in the schizolophous growth-stages of *Notosaria* and *Waltonia* (Atkins 1960, fig. 2; Rudwick 1962, fig. 6, 7a, 9a). The schizolophe of *Thecidellina* has not yet been described in operation. In a ptycholophe there are similar 'tunnels' in the lateral indentations as well; this has been seen in *Megathiris* (Atkins 1960, fig. 6). Lacaze-Duthiers (1861) only observed *Lacazella* with the filaments contracted frontally (text-fig. 7A), but their probable natural orientation can be inferred (text-figs. 7B, C) by analogy with *Megathiris*.

In all these schizolophes and ptycholophes the space near the dorsal valve surface is divided into two parts; the space corresponding to the lobes is filled with inhalant water, whereas the space corresponding to the indentations is filled with exhalant water. Water is filtered through the filament-row around the periphery of the lophophore, but also passes into the blind-ended tunnels in the indentations, from which it emerges peripherally (cf. Atkins 1960, fig. 6; Rudwick 1962, fig. 6).

The wide gape between the valve edges of *Megathiris* (and probably *Lacazella* also) is divided in effect into two apertures. The exhalant aperture extends all round the gape as a fairly narrow zone near the dorsal valve edge; the inhalant aperture occupies the remainder of the gape, nearer the ventral valve but not extending as far posteriorly. The apertures are separated only by the tips of the filaments around the periphery of the

lophophore. In principle there might be re-circulation around these apertural filaments; but in practice the wide opening of the shell exposes the periphery of the lophophore to sufficient external currents and turbulence to render any re-circulation insignificant.

It is reasonable to reconstruct the filaments of *Bactrynium* in a similar orientation, forming 'tunnels' across each of the indentations (text-fig. 7D). Then its current system would also have been similar (text-fig. 10). Water would have been drawn towards the dorsal valve surface, and would then have been filtered either through the filament-row around the periphery or else into the tunnels; within each tunnel an exhalant current would have flowed laterally or anteriorly to emerge near the edge of the valve. Thus in effect the part of the gape nearest the dorsal valve edge would have been an exhalant

A   B
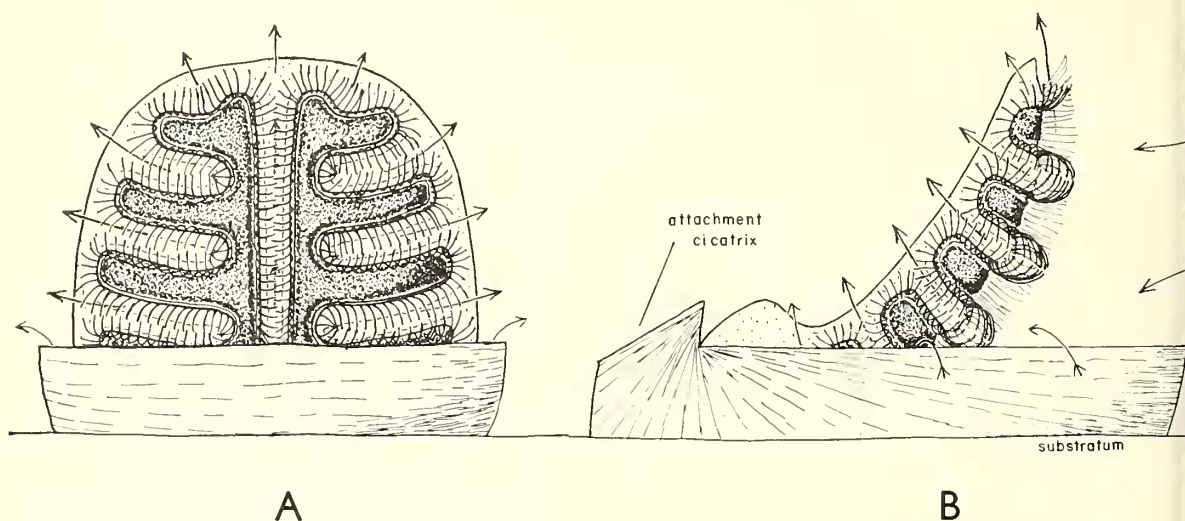
TEXT-FIG. 10. Reconstruction of *Bactrynium* in feeding position, showing inferred orientation of filaments, and consequent paths of inhalant and exhalant currents. A, anterior view; B, lateral view.

aperture, and the rest of the gape a wide inhalant aperture. Unless *Bactrynium* lived in exceptionally still water there would have been little risk of any substantial re-circulation of the water.

As in *Thecospira*, therefore, the observed morphology of *Bactrynium* is consistent with a ciliary feeding mechanism essentially similar to that of living brachiopods.

On this interpretation *Bactrynium* developed the ptycholophous alternative to a greater degree of elaboration than in any living brachiopod. This may be related functionally to its greater size. Observations on living brachiopods of various species and at various growth stages suggest that the pumping capacity of filaments is roughly

constant, as might be expected of a property dependent on a mechanism (i.e. the ciliary action) operating on the cellular level (Rudwick 1962, p. 611). But the pressure difference (between inhalant and exhalant chambers or spaces) at which a lophophore can operate is limited by the ability of the slender and unfused filaments to withstand the pressure and remain in position. Therefore if a blind-ended tunnel formed from two apposed stretches of filament-row were below some critical width, the rate at which water was being pumped into the tunnel might exceed the rate at which it could escape down the tunnel, and the water might then force the filaments out of position and flow back into the inhalant space. On the other hand it is clearly advantageous to the efficiency of the whole ciliary feeding mechanism that each tunnel should be as narrow as possible without incurring the problem mentioned above: for only so can the maximum total length of filament-row, and hence the maximum filtering capacity, be accommodated within a shell of given size. There must, therefore, be some optimal width for the tunnels, which would be the same for any normal ptycholophe. Similarly, it is clearly advantageous that the inhalant 'troughs' between the exhalant tunnels should also be parallel-sided and of some uniform width, so that as many as possible can be provided in a given space.

Thus the entire form of a ptycholophe can be interpreted as a means of maintaining the maximum effective filtering capacity within a shell of limited size. Any ptycholophe is inherently limited by being attached throughout to the mantle, so that its elaboration to provide greater filtering capacity can only be in two dimensions, making the best use of the *area* of the dorsal valve surface (cf. Rudwick 1962, p. 611). The only means of lengthening an attached filament-row within such a limited area is to buckle it into lobes and indentations. But if there are also definite optimal widths for these lobes and indentations, the lophophore must be elaborated during growth by the sequential addition of new lobes and indentations to an initially simple schizolophe. Hence it is to be expected that the degree of elaboration of the ptycholophe should be directly related to the absolute size of the dorsal valve, both during the ontogeny of a single species and also among species of different adult sizes. It should thus show 'size-required allometry' (Gould 1966). This seems to be true of *Bactrynium* as far as the limited number of specimens allows such a conclusion (text-fig. 5); and a comparison with some thecideaceans (text-fig. 11) shows that they too have lobes and indentations of about the same size.

Unfortunately, quantification of this allometric relation is hardly possible, in view of the difficulties of estimating the size of the true 'body' of a brachiopod, as opposed to the size of its mantle and shell.

AFFINITIES AND EVOLUTION

Affinities of Thecospira. Williams (1953*a*) pointed out that *Thecospira* had such strikingly strophomenide characters that it could not be excluded from that group solely because of its possession of a spiral brachidium, the only character which suggested affinity with the spiriferides. *Thecospira* was therefore included within the Orthotetacea (now Davidsoniacea).

Like the davidsoniaceans of the Palaeozoic, *Thecospira* was cemented by the ventral valve during the earlier part of its life history; it has a strophic hinge-line, well-developed

teeth and sockets, and a large rectangular cardinal process. Most Palaeozoic davidsonia-
ceans (except the earliest) are pseudopunctate, but *Schuchertella* is said to be impunctate
(Williams 1965, p. 408), and an apparently punctate structure has been reported in
Streptorhynchus (Thomas 1958). Against this background of diverse shell structure, the
existence of punctate, impunctate, and obscurely pseudopunctate species of *Thecospira*
is consistent with an argument for affinity.
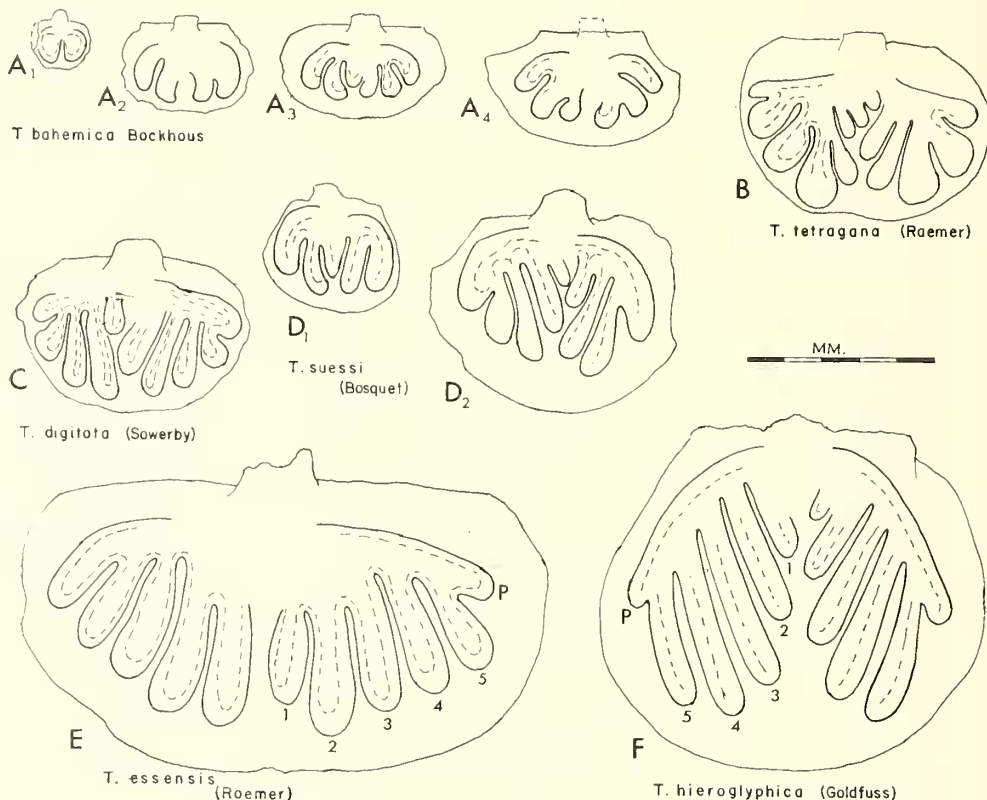
TEXT-FIG. 11. Drawings of the grooves and ridges on the dorsal valve of various species of *Thecidiopsis*,
to show the uniformity of dimensions of the lobes. All ×5; compare with *Bactrynium*, text-fig. 5.
(Sources: A, Nekvasilova 1964, pl. XI, fig. 4, 6, 8; pl. XII, fig. 5; B–F, Backhaus 1959, B, pl. 5, fig. 4;
C, pl. 4, fig. 2; D, pl. 7, fig. 1, 2; E, pl. 4, fig. 8; F, pl. 5, fig. 7.) Lobes of E and F marked with inferred
order of development; compare text-fig. 6C. Scale represents 5 mm.

Thecospira is exceptional among davidsoniaceans in having an 'entire' (i.e. plane)
pseudodeltidium (Williams 1965, p. H366), but this is a development that certainly
occurred several times among the strophomenides, and apparently related shells have a
convex pseudodeltidium. Likewise it has lost all but a faint trace of the costellate shell
surface characteristic of davidsoniaceans, but this too occurred in other strophomenide
groups (Williams 1965, p. H364). When the costellae are most clearly visible they show
a pattern of increase by intercalation, as in other davidsoniaceans, and not by lateral
branching. The pustular or spinule-bearing shell surface which apparently replaced the

costellae is not found, so far as I am aware, in any other davidsoniacean, and is more reminiscent of productaceans such as *Waagenoconcha*. But *Thecospira* lacks the larger tubular spines that seem to have been universal among the productaceans and strophalosiaceans.

The most important character distinguishing *Thecospira* from other davidsoniaceans is, of course, the spiral brachidium. But the unique structure of the lamellae suggests that the brachidium developed independently from those of the Spiriferida.

Spiral brachidia have recently been reported in *Cadomella* (Cowen and Rudwick 1966), which is generally regarded as related to the chonetaceans, so that there is now evidence that spiral brachidia evolved at least *twice* outside the Spiriferida. Even among the Spiriferida themselves spiral brachidia may have evolved more than once, the atrypaceans being in many respects closer to the rhynchonellides than to most other spiriferides (Copper 1965).

Palaeozoic davidsoniaceans probably possessed spirolophes supported by a hydrostatic or other 'soft' skeleton, for spiral impressions are known in *Davidsonia* itself. Davidsoniaceans existed in considerable abundance and variety even in Upper Permian time. The teeth of *Thecospira*, being unsupported by dental lamellae, suggest the Schuchertellidae or Orthotetidae as possible ancestors. The cardinal process and 'socket plates' have perhaps the greatest resemblance to those of *Streptorhynchus*; *Orthotetes* is another possible ancestor.

From some such Permian ancestor, the evolution of *Thecospira* would have involved (*a*) acquisition of brachidium (*b*) loss of convexity in pseudodeltidium and chilidium (*c*) obsolescence of costellae and (in some species) replacement by pustules, and possibly (*d*) loss of pseudopunctate structure and (in some species) acquisition of punctae. There is, however, no reason to suppose that these changes took place simultaneously. As already mentioned, the diversity of shell structure in *Thecospira* was foreshadowed in the Permian davidsoniaceans. Even the spiral brachidium may have evolved earlier than is yet apparent, and it might be worth examining Permian davidsoniaceans for any trace of the bases of crura. In any case, the evolution of *Thecospira* would not have involved any major changes in the relation of the shell to the substratum, in the hinge and musculature, or in the ciliary feeding mechanism. Only the supporting structures of the brachial axis would have changed, from a probably hydrostatic to a purely calcareous skeleton. As already suggested, there may have been an adaptive advantage in this change, in allowing a greater filtering capacity within a shell of given size.

The Koninckinidae, which have generally been regarded as abnormal Spiriferida, should probably now be placed with *Cadomella* as post-Palaeozoic descendants of the chonetaceans (Cowen and Rudwick 1966). Like *Thecospira*, the koninckinids are first known from Middle Triassic strata, but they are significantly different in the structure of the brachidium and many other characters. If this interpretation of koninckinids is correct, it implies that two relict strophomenide groups evolved spiral brachidia independently at about the same time, after most of the related 'normal' genera had become extinct.

Affinities of Bactrynium. As already mentioned, the affinities of *Bactrynium* have remained more controversial than those of *Thecospira*. Affinity to Lyttoniacea and to Thecideacea are interpretations that have been almost equally supported for many
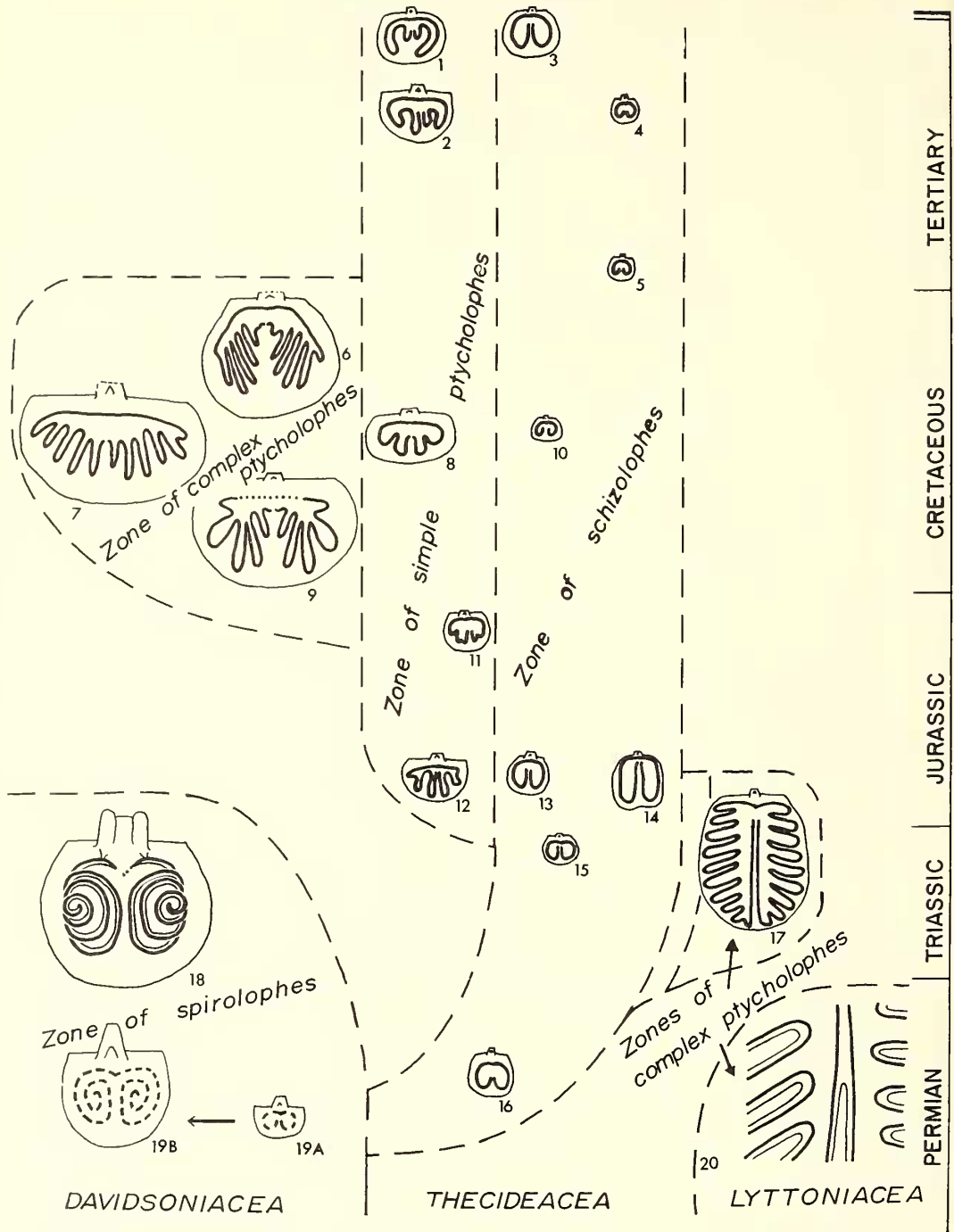
TEXT-FIG. 12. Diagram to show inferred phyletic and functional relationships of *Bactrynium* and *Theco-spira* to other brachiopods. Outlines of dorsal valves of respresentative species are shown at uniform